THE GROWTH OF FUNGI IN SOIL

J. S. WAID

Levington Research Station, Suffolk

Introduction

Saprophytic fungi and other heterotrophs which are active in the litter, humus, and mineral horizons of the soil exploit the energy-containing materials in decomposable organic matter, and bring about the release of nutrients locked up in the decaying substances. A significant proportion of these nutrients are taken up by photosynthetic plants, which utilize them in the production of the organic materials with which the energy intake of the community is maintained (Macfadyen, 1957). The efficiency of fungi in their utilization of available carbon substrates in the soil complex was appreciated by Foster (1949), who points out that soil fungi probably account for the bulk of the cell material that is formed by soil microbes. However, despite the ecological importance of the activities of filamentous soil fungi, we know little about the biology of the production and depletion of mycelium in the soil environment.

The characterization of soil-inhabiting fungi

Our knowledge of the events which occur in the soil is limited, like all other branches of ecological science, by the scope and the limits of accuracy of available techniques (Garrett, 1955). The amount of research which has been devoted to the study of soil fungi has been prodigious; in 1916, Waksman was able to refer to 125 publications, and Thom, in 1927, mentioned that the subject was expanding rapidly. Until recently it was mainly various groups of sporing fungi, in particular members of the Mucorales and the Fungi Imperfecti which grow well in artificial media, that had received detailed study (Chesters, 1949; Warcup, 1957). As investigators could not be sure that the sampled fungi were in a vegetatively active state or were taking part in soil processes, generalizations about the behaviour of single species of fungi in the soil environment could not be made (Harley & Waid, 1955*a*; Thornton, 1956; Warcup, 1955*a*, *b*).

Many important developments in the study of the fungus flora of the soil have evolved from attempts to classify the behaviour of soil-

inhabiting as well as mycorrhizal and parasitic root-infecting fungi (Garrett, 1944, 1950, 1951, 1952, 1956*a*; Harley, 1948, 1950, 1952; Waksman, 1916, 1917, 1944). The grouping of fungi on the basis of their ability to utilize chemical substrates such as lignin and cellulose has been developed as a system of ecological classification by various authors (Thom & Morrow, 1937; Burges, 1939; Chesters, 1948; Garrett, 1951). Such 'substrate groups' have been characterized by Garrett (1956*a*) as possessing 'some special physiological or biochemical attribute conferring a competitive advantage for colonization of a particular substrate'. Similarly, Stanier (1953) emphasized that the many kinds of substrate present in the soil are each colonized by a characteristic and limited range of organisms, each with its individual nutritional requirements. He also stressed that the environments of free-living micro-organisms are micro-environments, and such micro-environments occur everywhere, for example cellulose fibres.

The distribution of fungi in the soil has been graphically described by Garrett (1955) as 'a three-dimensional pattern of substrates'. Each substrate 'passes in its turn through the successive phases of colonization, exploitation, and exhaustion'. When the capacity of the micro-habitat to support further life is reduced to zero, only those surviving resting cells, or mycelia growing outwards through the soil, mark the sites of former substrates.

The examination of the behaviour of fungi in the soil environment in the presence of organisms which are antagonistic towards them has been the basis of many recent studies. 'Competitive saprophytic ability' has been defined by Garrett (1956*a*) as the 'summation of physiological characteristics that make for success in competitive colonization of dead organic substrates'. Park (1958) has pointed out that the various kinds of antagonism which occur between associated pairs of species include antibiosis, parasitism and predation as well as competition for the same object in the environment.

Various criteria that have been employed to designate a fungus as a soil inhabitant have been resolved by Park, who defines such a fungus as 'an ecological saprophyte . . . able to continue its existence and activities in the soil, colonizing and utilizing decomposable dead substrata, and maintaining itself alongside other members of the soil population, without the necessity of an interposed parasitic phase'. The last phrase in Park's definition could be modified to read 'without the necessity of an obligate association between a fungus and a living host organism'.

Other fungi occurring in the soil: Other fungi which occur in the soil

and contribute to the ultimate breakdown of organic materials, but which do not qualify as soil inhabitants, are called *soil invaders* (Waksman, 1917). They are also called *allochthonous* fungi by Saitô (1955*a*) and *exochthonous* fungi by Park (1957*b*). Soil invaders do not possess the ability to develop or maintain themselves in an active condition in the soil environment. They are, in general, unable to colonize dead organic materials in the soil, although their propagules will ensure their survival in an inactive state. Even so, their hyphae can survive in dead organic materials provided they do not succumb to the antagonistic activities of other members of the soil population.

Soil invaders can be subdivided into two groups on the basis of the habitats in which they grow. The first group is formed by fungi which utilize substrates not developed within the soil. An example is the fungus *Pullularia pullulans*, which colonizes deciduous leaves as an epiphyte, but which ceases to be active soon after the leaves fall (Smit & Wieringa, 1953). The second group is made up of two kinds of *root-inhabiting fungi*, namely specialized root parasites and mycorrhizal fungi. Of the latter, only the ectotrophic and not the endotrophic forms will be considered here.

The growth and survival of the root-inhabiting fungi is mainly confined to the surfaces and the tissues of the root of their host plants. The association with their hosts is manifest only when such factors as soil conditions, host physiology, competition from other organisms, the state of the fungal inoculum, etc., are suitable. Many root-inhabiting fungi are capable of ectotrophic growth over the surfaces of the host root without penetrating the host tissues and so can co-exist with other rhizosphere and root-surface organisms inhabiting the root region. Thus a parasitic or a symbiotic association with the higher plant is not necessarily the eventual outcome of the presence of root-inhabiting fungi on the root surfaces of a host. But their low competitive saprophytic ability imposes a restriction upon the spread of such fungi from host to host *via* the soil.

Root-inhabiting fungi can colonize new hosts by two methods. The first is by root contact between neighbouring pairs of plants, and the second by the spread of hyphae or mycelial aggregates, for example rhizomorphs, from the tissues of infected host plants, which are utilized as a food base. The success of the latter method of root infection is limited by the size, number and nutritional status of the infecting units. It has been shown that the maximal radius for spread of mycelium from a food base is greater than the maximal radius for successful infection (Garrett, 1956*a*).

Studies of the growth of fungi in the soil environment

Some recent studies on the growth of fungi in non-sterile soil are discussed in the remaining three sections. The first describes some of the attributes which enable fungi to grow in the soil. The material under review relates to the reactions of fungal isolates to certain factors in the soil environment, and is derived mainly from experimental observations made under controlled conditions. The growth of soil fungi in pure culture experiments is not discussed as several excellent accounts exist (Foster, 1949; Hawker, 1950, 1957; Lilly & Barnett, 1951; Wolf & Wolf, 1947).

The second section is devoted to conclusions obtained from field surveys of the growth of mixed populations of fungi. The situations which are described were generally complex, and the effects of the many animate and inanimate components of the ecological environment were not resolved.

The third section is concerned with various factors which influence the production and depletion of mycelium in soils.

1. OBSERVATIONS ON THE PATTERN OF GROWTH OF SOIL-INHABITING FUNGI

Germination. Dobbs & Hinson (1953) and other authors (Chinn, 1953; Hessayson, 1953; Jackson, 1958; Jefferys & Hemming, 1953; Molin, 1957; Stover, 1955) have described a fungistatic factor in the organic horizons of the majority of the temperate and tropical soils studied. This factor, which is diffusible in the soil solution, inhibits the germination of fungal spores buried in the soil, although such spores germinate when placed in distilled water or in nutrient solutions. The chemical nature of this factor is unknown. Its effects can be temporarily nullified by the addition of a critical concentration of glucose or easily decomposable organic materials to the soil. Although it appears to be of biological origin, the evidence indicates that it acts not as an antibiotic (Dobbs & Hinson, 1953) but as a competitive inhibitor to the enzymes concerned in carbohydrate metabolism. It is possible that the reaction of the fungus spores to this factor brings about a reduction in the wastage which would follow germination of fungal propagules in the absence of organic matter suitable for supporting growth.

Broadbent & Norman (1947) demonstrated that the addition of fresh organic material to soil accelerates the rate of decomposition of materials already present in the soil. Burges (pers. com.) suggests that this phenomenon could be partially explained by a local and temporary reduction

of the fungistatic effect sufficient to permit microbial attack on organic matter. Such a reduction in the fungistatic effect may accompany the increase in fungal activity which follows soil cultivation (Guillemaut & Montégut, 1956, 1957; King, Hope, & Eaton, 1934; Warcup, 1957).

Buxton (1957*a*) and Kerr (1956) have demonstrated variation in the behaviour of root-disease fungi during the pre-penetration stages of the infection of their host plants. It is of interest that Jackson (1957) has shown that spores of five species of soil fungi will germinate in rhizosphere soils, and that their germ tubes, with the exception of one of the species studied, show a tropic response to plant roots. It is conceivable that dextrose, fructose, or other energy sources are liberated in sufficient quantity in the root region to eliminate the fungistatic factor present in the surrounding soil.

Colonization of soil substrates. Once fungal propagules or mycelia start or renew growth, then the duration and the nature of the response to stimuli may determine the success of such fungi in exploiting chemical substrates suitable for growth. In general, the rapidity of the response of a soil-substrate colonist seems to depend upon its potential enzyme complement and the availability of nutrients for the generation of active protoplasm. Park (1954) found that the duration of such responses or 'induction' phases depends upon the size of the fungal inoculum and the nature and quantities of the food materials which are available. Waid & Woodman (unpublished) have observed that the duration of the period between the insertion of inert materials into soils and their initial colonization by hyphae can be shortened by increasing the temperature.

Colonization by fungi developing from spores. Few mucoraceous Phycomycetes can utilize carbon sources more complex than simple sugars (Jefferys *et al*, 1953). The typical response of their spores to the addition of fresh organic matter to soil is rapid germination and colonization of the material in precedence over other soil fungi. Their duration as active mycelia is probably very short, but their high metabolic rate enables them to exploit the available materials successfully.

The remaining fungi that develop from spores in soil colonize decomposable materials less rapidly than the Phycomycetes. These fungi are mainly cellulose-decomposing Ascomycetes and Fungi Imperfecti (Garrett, 1951), and it is the production of suitable cellulases that probably delays their colonization of substrates containing cellulose (Siu, 1957).

Chinn (1953) and Park (1954, 1955, 1956) demonstrated that even after the addition of decomposable organic materials to soil, most of the fungal spores decomposed rapidly, and that those which germinated

were either destroyed by the activities of other soil organisms or produced chlamydospores in response to the adverse environment. The survival in soil of the spores of soil-inhabiting and soil-invading species of fungi in a variety of ecological conditions has been studied by Park (1955, 1957*a*, *b*), who showed that the soil-invaders were incapable of colonizing organic materials buried in soil in the presence of antagonists.

Tribe (1957) has recorded that when a cellulose film is buried in soil, it is first of all colonized and exploited by cellulose-decomposing fungi. He observed no evidence of antagonism between fungal colonies exploiting the cellulose, and also that bacteria and soil mites were mainly responsible for the decomposition and disappearance of fungal hyphae. He never observed the reappearance of saprophytic fungi as colonizers of the cellulose residues. The inability of fungi to recolonize organic matter in soil may account for the difficulty of demonstrating the presence of active hyphae in humified organic matter.

Colonization by fungi equipped with relatively large food reserves. An interesting correlation between the size and the potential resistance of a host plant and the degree of specialization of the structures employed during colonization by root-infecting fungi has been described by Garrett (1956*a*). The concept implies that a fungus which colonizes materials containing chemical substances resistant to decomposition, such as lignin and cellulose, has severe difficulties to overcome. The development by an induced or inherent biochemical synthesis (Sussman, 1957) of enzymes capable of utilizing the available substrates necessitates a supply of suitable nutrients and energy-containing materials (Brown & Wood, 1953; Norkrans, 1950). As such fungi generally colonize materials previously occupied by species with high growth rates, nutrients are in short supply. The late arrivals have therefore to resort to translocating nutrients from a suitable food base. They also have to combat antagonism from other organisms, and it is conceivable that some part of their nutrient supplies are utilized to develop protoplasm and structures resistant to the effects of antibiosis, fungistasis, and parasitism.

Blair (1943) showed that the establishment of *Rhizoctonia solani* was dependent on the size and nature of the available food base. His results do not prove that this fungus relied upon a translocatory system, but that the food base was necessary to enable establishment in the soil environment.

Lignin decomposition is brought about mainly by Basidiomycetes, which form either mycelial strands or rhizomorphs. Factors which affect the success or failure of such fungi to colonize a fresh substrate have

been shown conclusively to be the quantity of nutrients available at the food base, the length and efficiency of the translocatory system, and the resistance of the organic materials to mechanical penetration and to enzyme attack (Garrett, 1956*a*, *b*).

Exploitation and exhaustion of soil substrates—mycelial growth. The rate of fungus growth in a uniform soil environment has been found to be independent of its inoculum potential during the colonization phase (Blair, 1943; Park, 1954). However, the time taken to exhaust a substrate depends upon the number of active hyphae capable of penetrating and decomposing the material under attack. Waid & Woodman (1957) found that soon after growth had begun upon nylon gauze buried in soil, a maximum rate of branching was attained, and shortly afterward most meshes (that is, sites available for colonization) became occupied. The relatively high surface to volume ratio of individual hyphae in the three-dimensional system of branching developed by filamentous fungi presents a large interface accessible to changes in outside conditions and for rapid exchange of materials between hyphae and soil. This system enables the production of sufficient quantities of enzymes, for example carbohydrases, in loci situated on the cell surfaces for conversion of extracellular substances to a form which can be assimilated by the cell if conditions are favourable (Hawker, 1957; Rothstein, 1954; Sussman, 1957).

Heterokaryosis. Heterokaryosis—the multiplication side by side of two or more genomes in a common cytoplasm—is a genetic mechanism unique to fungi which may be of importance during the exploitation phase of soil substrates (Stanier, 1953; Shepherd, 1957). The proportions of the various nuclear strains may be adjusted by their differential multiplication, thus conferring considerable plasticity on the genotype of the growing mycelium in relation to adaption to external conditions (Jinks, 1952; Pontecorvo, 1949). There is evidence that nuclei conferring pathogenic properties may develop incorporated in a mycelium containing nuclei of a type allowing a fungus to survive as a soil saprophyte (Buxton, 1954; Park, 1958; Rishbeth, 1955). Heterokaryosis may be a mechanism whereby the mycelia of Ascomycetes and Fungi Imperfecti, by adjustment of the nuclear population within their hyphae, can remain active for considerable periods in a changing ecological environment such as decomposing organic materials. In theory, species which do not possess a mechanism permitting variation of the genotype are at a disadvantage when exploiting a changing substrate in competition with a heterokaryotic species.

Translocation. The experimental studies of Schütte (1956) on the trans-

location of various substances within fungal colonies are of interest. The hyphae of *Aspergillus* and *Penicillium* were found to be incapable of translocation, and no streaming of their protoplasm was observed. The contrary was recorded for Phycomycetes and Basidiomycetes (cf. Melin, 1953), where the translocated materials accumulated in the apical regions of growing hyphae and streaming of their protoplasm was observed.

Soil-inhabiting fungi have been recorded as exhibiting a variety of types of growth habit (Chesters, 1948, 1949). This variation may be related to the degree to which the fungi can translocate nutrient materials. For example, soil fungi such as the Penicillia have short periods of vegetative growth followed by sporulation with the production of great numbers of spores. On the other hand, soil Basidiomycetes exist mainly in a mycelial state with the elaboration of complex translocatory structures formed by mycelial aggregation (Garrett, 1956*a*, *b*; Warcup, 1957).

Survival of soil fungi. Variation in behaviour of soil fungi appears to be related to the manner in which individual species survive to colonize fresh soil environments. The two methods of survival adopted by soil fungi can be either passive or active, and their development depends qualitatively and quantitatively upon the nutritional status of the mycelium. Passive methods of survival, such as by sclerotia or spore formation, are employed when the level of nutrition is adequate and antagonism is not excessive (Hack, 1957). When food supplies are depleted or other growth conditions are adverse, the existing protoplasm and nutrients within the hyphae are modified as chlamydospores, resting hyphae, or oidia. For example, mycelia colonizing nylon gauze buried in soil have been observed to start to form chalmydospores soon after the surfaces of their hyphae have become colonized by soil bacteria (Waid & Woodman 1957, cf. Ram, 1952). Similarly, active methods of survival involve the development of translocatory structures such as rhizomorphs and mycelial strands when nutrition is adequate, but 'starvation growth' often entails linear spread by infrequently branching and rapidly growing hyphae (Hawker, 1957). An indication that the active survival of soil fungi depends on the presence of a substrate which will support growth is afforded by the fact the hyphal filaments traversing soil pores generally lack protoplasmic contents (Jones & Mollison, 1948) and are non-viable, whereas a high proportion of hyphae isolated from organic materials will grow in culture (Warcup, 1951, 1957). The survival of soil-invading fungi in decomposing substrates depends in part upon the environmental conditions being adverse for the develop-

ment of antagonistic organisms (Dimbleby, 1953; Downie, 1943; Fellows, 1941; Rishbeth, 1951).

2. OBSERVATIONS ON THE GROWTH OF MYCELIUM IN VARIOUS SOIL ENVIRONMENTS

Macro-habitats for fungal growth. The surface vegetation has a considerable influence on the soil mycoflora. When a virgin soil habitat such as the fore-dune of a sand-dune system becomes colonized by higher plants, there is a parallel development of a fungal flora (Brown, 1958; Saitô, 1955*b*; Webley *et al.*, 1952). Changes in the composition of the surface vegetation, such as forest cover (Saksena, 1955; Tresner *et al.*, 1954), or an agricultural crop (Guillemat & Montégut, 1956, 1957) are also accompanied by changes in the composition of the soil flora. The effect is due partly to the accumulation of organic residues from the developing association of plants and animals, and partly to the development of a rhizosphere and root-inhabiting flora associated with the species of higher plants. The influence of a single species is illustrated by the development of a rich flora of soil-borne parasites when badly managed monocultural systems of agriculture are employed.

In general, fungi abound in well-aerated organic horizons of the soil (Warcup, 1951*a*), but it is not yet certain which species are most active in exploiting the different types of decomposable material which occur in the soil.

Micro-habitats for fungal growth. Chesters (1949) considering existing information on micro-habitats for fungal growth, mainly obtained by Kubiena (1938), suggested that attention should be paid to the growth of fungi such as *Pythium*, *Rhizoctonia*, the larger Ascomycetes, Basidiomycetes, and the darker-coloured Hyphomycetes associated with organic debris in the soil. Saitô (1956), Stenton (1953), and Warcup (1951*a*, *b*, 1955*b*, 1957) have each provided evidence that Basidiomycetes and sterile mycelia are active in certain horizons of undisturbed and cultivated soils. Thornton (1956) observed that *Rhizoctonia* occurs in a mycelial state in natural grassland soils, and formed 49% of his isolates on screened-immersion plates. Warcup (1955*a*, 1957*b*), by analysis of the origin of individual isolations from soil, found that Basidiomycetes, Rhizoctonias, and sterile fungi, especially those with dark-coloured hyphae, form the main component (70%) of the population of viable hyphae in a wheat-field soil.

On the other hand, the species of the Mucorales and the Fungi Imperfecti, which are recorded as predominant in soil (Gilman, 1957)

and which belong to such genera as *Mucor*, *Absidia*, *Mortierella*, *Aspergillus*, *Cladosporium*, *Fusarium*, *Penicillium* and *Trichoderma*, were generally isolated by Warcup from passive survival structures. On the few occasions when species of the above-mentioned genera were isolated from hyphae they were present either upon plant débris or on decomposing residues which had been ploughed in. Such observations on the active compoents of the soil population correlate well with those of Tribe (1957) who, when following the fate of cellulose in soil, found few of the above-mentioned genera, but noted a restricted flora of species not generally considered (Siu, 1951) to be abundant on decomposing cellulose.

Substrates in soil exert a selective effect on their associated microflora, an extreme example being the complete dominance of ectotrophic mycorrhizal fungi on the surfaces of infected tree roots (Harley, 1948). Various techniques have been used to study the microflora colonizing soil substrates, and a selection of roughly comparable results of surveys of active mycelia on root surfaces is given in Table 1.

A general observation derived from the table is that sterile fungi and occasionally Basidiomycetes are very abundant on lateral roots; that is, small inocula which bear few antagonists. Sporing fungi increase in abundance as the roots age, and are so numerous on tap roots that it may be that they are involved in minor ecological successions on senescent cortical tissues. For example, such fungi as *Cylindrocarpon*, *Mortierella*, and *Mucor rammanianus* are particularly abundant on the surfaces of roots with secondary thickening. Fusaria, on the other hand, abound on the roots of pasture plants with decomposing cortical tissues.

Harley & Waid (1955*a*, *b*) have shown that the fungal population of root surfaces varies with the distance from the root apex, the age of the plant, the soil, and the conditions for growth (for example, light intensity).

The composition of root surface populations can vary considerably over very short distances. The course of the fungal invasion of two layers of plant tissue, the inner and outer cortex of decomposing roots of rye-grass, has been studied by Waid (1956, 1957). Sterile species of fungi were the dominant initial colonists, and they were gradually replaced by *Fusarium culmorum* and other succeeding groups of fungi which grew into the cortex.

It is frequently found in surveys of this nature that a single fungus species grows from adjacent fragments of root, especially on the older portions of root systems (Harley & Waid, 1955*a*). If it were known whether such growth represented one or several separate mycelial

colonies a significant contribution would be made to the knowledge of the growth and development of fungi in soil habitats. A possible approach might be by a combined study of the distribution of mycelia and of fungal mating-type factors as employed by Burnett & Partington (1956) for the higher fungi.

TABLE 1

The most abundant fungi isolated from the surfaces of living roots of several species of plants.

Host and Roots Sampled	Most Abundant Fungi	Author
Pinus sylvestris —lateral	*Mycelium radicis atrovirens* *Pyrenochaeta terrestris*	Robertson (1954)
Fagus sylvatica —lateral —tap	Sterile mycelia including *Mycelium radicis atrovirens* *Cylindrocarpon* sp.	Harley & Waid (1955*a*)
Fraxinus excelsior —tap	*Cylindrocarpon* sp. *Rhizoctonia* (?)	Kürbis (1937)
Pisum sativum —tap	*Fusarium* sp. Mucorales	Buxton (1957*b*)
Pisum sativum —tap	*Cylindrocarpon* sp. *Fusarium* sp.	Stenton (1958)
Trifolium repens —tap	Sterile mycelia *Fusarium* sp. *Cylindrocarpon* sp.	Waid*
Dactylis glomerata —fibrous	*Fusarium* sp.	Waid*
Lolium perenne —fibrous	*Fusarium* sp. Mucorales	Waid (1957)

* Unpublished work.

3. MYCELIUM PRODUCTION AND DEPLETION IN SOIL

Consumption of nutrient supplies. Several attempts have been made to estimate the relative importance of micro-organisms and fauna in the breakdown of organic matter in soil. The estimates agree in that fungi and heterotrophic bacteria, together with nematodes and protozoa, form the major part of the living material in soil. Because the respiratory rates of soil fungi are higher than that of soil animals and because they require external substrates for growth, the general conclusion has been that soil fungi are among the main primary consumers of decomposable material in soil (Birch & Clark, 1953; Macfadyen, 1957; Russell, 1950).

The energy-containing materials which support the growth of soil

fungi become available to them in two ways. One is where the communal consumption of energy is balanced by a continuous inflow of energy-containing materials. Such a state occurs, for example, in the root region of plants. Here organic materials are being continuously released from the plant roots in sufficient quantity to maintain the growth of root-surface and rhizosphere fungi. The second way is where the flow of energy is not maintained and where the activity of the heterotrophs is limited by the energy content of the habitat; for example, an annual leaf fall. In a given soil locality it is not yet possible to estimate the rate at which energy-containing materials are utilized, either in the synthesis of mycelia or in fungal respiration. Such estimates would be important in terms of the effect of the soil microflora on the growth and nutrition of higher plants. Apart from the beneficial activities of the soil microflora in making plant nutrients available to higher plants, there are also competing activities. One is the drain on nutrients required for the maintenance of the cell mass of the soil microflora (Nilsson, 1957). Another is the conversion of plant nutrients to forms which are unavailable to the higher plants; for example, the nitrogen in the glucosamine units of fungal chitin. The activities of higher plants and soil flora are interdependent and, perhaps their influence upon one another is mainly through the rhizosphere.

The few estimates which have been made of the efficiency of higher fungi as consumers of simple substances show that under pure culture conditions a variety of Ascomycetes and Basidiomycetes, especially those inhabiting forest litter, have considerable biosynthetic potentialities, and that a large proportion (as much as 65%) of their substrate can be converted to mycelium (Gray & Bushnell, 1955; Mikola, 1956).

Influence of non-biological factors

Temperature. The maximum temperature for growth of mesophilic fungi lies between 35° and 40° (Brown & Wood, 1953), so it would be expected that the rate of fungal growth would fall off sharply in summer months in the surface layers of British soils where temperatures can exceed 35° (Russell, 1950). Various reports that fungi can cause damage to snow-covered plants (Lebeau & Cormack, 1956) are indirect evidence that certain species of fungi can flourish in soil at low temperatures. Waid & Woodman have observed that the rate at which nylon gauze buried in organic soils at various altitudes (300–900 m.) is colonized by fungal mycelium decreases with an increase in altitude. These results were not thought to be due entirely to the influence of soil temperature, but an experiment carried out during July 1957 in moist humus shaded

by a yew tree and repeated at the same site in December showed that activity fell off in the colder season. As this decreased activity was only 43% of that observed in summer, it was concluded that fungi are still active in the humus layers of forest soils during winter months. Laboratory investigations showed that mycelium would steadily accumulate on gauze buried in soil at temperatures from 13°–25° over a period of 8 days, but at 30° there was no accumulation after 2 days' incubation and none at 2°. The apparent lack of hyphal activity over the period from 2–8 days in the soil held at 30° may have been due to two processes which are accelerated by an increase in temperature. The first of these is the exhaustion of available substrates for growth with perhaps the accumulation of staling products. Secondly, breakdown of senescent and dead hyphae by other soil organisms giving the false impression that active hyphal growth has ceased or decreased in rate. The results agree with Fellows' (1941) observations that soil conditions which support growth of an organism are not necessarily optimal for survival from antagonists.

Moisture. When the water content of a soil either falls below the wilting percentage (Mitchell, Adams & Thom, 1941) or becomes sufficiently great to impede soil aeration there is a great reduction in the active growth of fungal hyphae (Waid & Woodman, unpublished). Warcup (1957) found negligible activity in an Australian wheat-field soil during the dry season. He observed a relatively high rate of survival among fungi isolated from humus particles which probably afforded a certain degree of protection against desiccation, but he could not determine whether fungi survived in the humus particles in an active or passive state. With rain, fungi became very active, and after a few days there was a large increase in the proportion of viable hyphae which could be isolated from the soil, and at the same time several species of mould fungi had sporulated abundantly.

Stover (1953) reports a reduction in the ability of Fusaria to survive in soils held at high moisture contents, where the multiplication of soil bacteria is favoured at the expense of the nutrient and oxygen supplies of soil fungi. Reduction in soil aeration would influence the growth of strongly aerobic fungi, but Kubiena (1938), Boswell & Sheldon (1951), and Stover have noted the abundance of *Hyalopus*, *Cephalosporium*, and various other species of fungi in water-logged soils. Blair (1943) noted a reduction in the growth of *Rhizoctonia solani* in soils held at high-moisture contents. The growth of the fungus at these high-moisture contents was least in soils with small-sized particles, where presumably the reduction in soil aeration was most marked.

Soil reaction. Soil pH affects the availability of nutrients in the soil. It is possible that it also influences the physiological functioning of the fungal thallus, possibly through its effect on the reactions occurring on the cell surfaces rather than through a direct influence on the internal processes of the cell.

The optimum pH for the growth of *Rhizoctonia solani* in soil was found by Blair (1943) to be at about 7·0. Warcup (1951) recorded that more species of fungi abound in neutral than in acid or alkaline grassland soils. He observed that a few species had a high-sporing capacity in the acid soils, which may account for the records of large numbers of mould fungi in acid soils obtained by the dilution-plate technique. Bacterial decomposition of senescent and dead hyphae may proceed more rapidly in alkaline soils than in acid soils, and may thus keep the quantity of mycelium at a low level in alkaline soils.

Carbon dioxide and oxygen concentration. Burges & Fenton (1953) studied the effect of carbon dioxide and oxygen on the growth in culture of a variety of mould fungi isolated from various horizons of a soil profile. Their results show that fungi abundant in surface horizons were intolerant of carbon dioxide, but those abundant in subsurface horizons, where carbon dioxide can accumulate in the field (Russell, 1950), could tolerate carbon-dioxide concentrations as great as 10% by volume. These authors found no differential effect of oxygen on the growth of their various isolates.

Size of soil-pore spaces. Kubiena (1938) made some interesting observations on the comparative morphology of fungi inhabiting soil spaces where he found that in general there was a reduction in the size of the fruiting structures of sporing fungi with decrease in pore size. The dimensions of these fruiting structures were much smaller than those recorded for specimens grown in culture.

Durability of fungal mycelium. The hyphae of Phycomycetes do not appear to be very resistant to decay, and soon disappear in the soil. At the other extreme, the hyphae of Basidiomycetes seem to be highly resistant, especially to adverse conditions such as drought (Warcup, 1957). They are more resistant than Phycomycetes to bacterial or actinomycete attack, and the dark-coloured hyphae of certain species appear to endure for a long time in the soil (Tracey, 1956). In forest soils mycelial wefts, rhizomorphs, and mycorrhizal roots are visible evidence of the abundance of Basidiomycetes, yet little is known about the rates of production and decomposition of their mycelia. Waid & Woodman (unpublished data) have noted that the proportion of dark-coloured mycelia, hyphae with clamp connexions and rhizomorphs, colonizing

nylon gauze buried in woodland soils increased with the duration of the exposure period. After a year such mycelia formed from 80–100% of the mycelial populations on the gauze, but the viable proportion was not determined.

Interactions between soil fungi and soil fauna. The interactions between saprophytic soil fungi and the soil fauna is a neglected field of study due perhaps to the difficulties of sampling methods, the identification of species and the development of suitable techniques for the measurement and comparison of their relative activities (Waid, 1959). A few aspects of this topic in so far as they affect the growth of fungi in soil will be very briefly considered here.

The mixing of plant remains from the litter layer of the soil with lower soil horizons is mainly brought about by soil animals. Such activity probably increases the rate of breakdown of decomposable materials because in the litter layer environmental conditions such as moisture régime, humidity, light intensity, and diurnal fluctuations in temperature are less favourable for microbial growth than in the other biological horizons of the soil, especially in dry seasons (Macfadyen, 1957). Comminution of plant remains by litter-feeding animals almost certainly facilitates decomposition by breaking down the hard tissues and making the organic matter more readily available to the soil microflora (Birch & Clark, 1953; Winston, 1956). The activities of soil animals and fungi must initiate a multiplicity of linked processes and biological successions on fragments of organic materials (Murphy, 1956), which cannot be satisfactorily studied by present methods. Many food chains of soil animals seem to depend upon an initial attack on plant remains by soil fungi; in fact, fungi form the main constituent of the diet of many members of the soil fauna, especially of species of mites and nematodes (Birch & Clark, 1953; Park & Auerbach, 1954). It is possible that the estimation of the consumption of fungal mycelium cropped by and supporting the growth of a population of soil animals may be one way of estimating part of the mycelium produced in the soil.

Jacot (1939) and Winston (1956) have both shown that the succession of animals in decaying plant tissues is influenced by the nature of the decay and the palatability of the fungal mycelia. Twinn & Waid have gathered together information shown in Table 2 concerning the biology of the invasion of decomposing oak-leaf litter obtained from a series of experiments concerned with the breakdown of forest litter (Capstick, 1956; Gilbert, 1957). The results show that the relative quantities of mycelia and nematodes do not remain constant but vary with season. It is possible that an accumulation of hyphae on the leaves was prevented

by the activities of other organisms including nematodes, the majority of which were found to be fungal feeders. Winston (1953) recorded that soil animals were agents in the dispersal of fungi in decaying plant materials in soil, and that established fungal mycelium grew actively and was repeatedly cropped by successive populations of soil animals.

TABLE 2

The invasion of decomposing oak leaves by fungi and nematodes. Leaves collected during leaf fall 1956 *and laid down in November*

	Length hyphae/ microscopic field in mm. Mean 20 fields sample size = 6 leaves	Number of field with hyphae Total 20	Number of nematodes/g. dry weight of leaf. Sample size = 12 leaves
November, 1956	0	0	0·3
December, 1956	1·4	3	1·8
January, 1957	4·0	7	5·4
February, 1957	3·5	9	9·9
March, 1957	2·6	8	9·4
April, 1957	2·0	8	1·7
May, 1957	1·8	8	15·5
June, 1957	4·0	9	10·3
July, 1957	5·4	10	37·1
August, 1957	4·0	10	43·5
September, 1957	13·3	10	—*
October, 1957	8·8	14	—*
January, 1958	2·6	7	—*

* Not sampled.

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